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Substrate Specificity of Hexokinases*

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For many years, investigations of the specificity of enzymes have been carried out in a number of different laboratories. From such studies much has been learned about the mechanism of action of enzymes, the nature of the active site, and the nature of the enzyme-substrate complex. For enzymes acting on polyhydroxy compounds such as glucose, it has been possible to visualize the enzyme-substrate complex involving hydrogen bonding at several points, thus conferring on the union a rigidity in space necessary for stereochemical specificity of reaction.

Although hexokinases derived from various rat tissues have been studied, the reports do not permit definite conclusions to be drawn concerning differences in the enzymes and their specificities. Rat intestinal mucosa has been studied by Hele (1), Sols (2), and Long (3). The activity of rat kidney hexokinase toward glucose, fructose, and mannose has been reported (3–5), and rat liver has been studied extensively by many workers (3, 6–9) in regard to fructokinase and glucokinase activity. There is agreement that fructokinase will not phosphorylate glucose and that liver must also contain a gluco- or a hexokinase in addition to the fructokinase. This hexokinase has not been isolated or characterized.

In the present paper, the substrate specificities of hexokinase preparations from rat intestine, kidney, and liver have been investigated with a view to finding which groups of the polyfunctional carbohydrate molecule appear to be involved in the enzyme-substrate complex.

Studies of phosphorylation of D-glucose, some rare D-aldohexoses, D-glucosamine, *N*-acetylglucosamine, and 2-deoxy-D-glucose were made. The findings indicate distinct differences in the specificities of the enzyme preparations.

EXPERIMENTAL PROCEDURE

Methods and Materials—The sugars used were obtained commercially or prepared synthetically as follows: glucosamine hydrochloride was obtained from Pfanstiehl Laboratories; *N*-acetylglucosamine was obtained from Chas. Pfizer and Company, Inc.; 2-deoxyglucose was obtained from Aldrich Chemical Company, Inc. These substances were recrystallized before use. The rare aldohexoses were prepared from their corresponding lactones by modifications of the procedures of Sperber *et al.* (10) and Isbell *et al.* (11). Allonolactone and calcium altronate were prepared from ribose according to the procedure of Pratt and Richtmyer (12). Gulonolactone was prepared from xylose by the procedure of Isbell (11). Talonolactone was prepared from γ-galactonolactone by epimerization with pyridine according to the procedure of Glatthaar and Reichstein (13). ATP was obtained from Pabst Laboratories as the disodium salt. EDTA[1] was obtained from the Eastman Organic Chemicals Division of the Eastman Kodak Company. Tris was obtained from Nutritional Biochemicals Corporation.

Assay Procedure—The method used for assaying the various hexokinase preparations was the constant pH microtitrimetric procedure of Schwartz and Myers (14). Incubations were carried out in 4-ml volumes at 30° and pH 7.4 with 0.02 M $MgCl_2$, 0.002 M ATP, 0.002 M EDTA, enzyme, and varying concentrations of hexose. A unit of enzyme was defined as the amount of enzyme required to produce 1×10^{-6} acid equivalents per minute at 30°. Phosphatase and ATPase activities were inhibited in the assay by the use of 0.02 M fluoride (3, 15, 16) or *n*-octanol (17). Freezing and thawing of the hexokinase preparations also served to decrease phosphatase and ATPase activity (17).

Enzyme Preparation—All enzyme isolation work was performed at 0 to 5°, unless otherwise stated. Male Sprague-Dawley strain rats were used as the tissue source. Protein determinations were carried out by the method of Lowry *et al.* (18) or by digestion and nesslerization as described in Hawk, Oser, and Summerson (19), after dialysis against running water for 15 hours.

1. Liver Hexokinase—Crude rat liver hexokinase was prepared as needed, since the preparation was stable for only 2 to 3 days when stored at −15°. To prepare the enzyme, two fasted rats were killed by snapping the cervical cord. The livers (approximately 20 g of tissue) were rapidly removed and homogenized in a Waring Blendor for 3 to 5 minutes with a buffer consisting of 2 volumes of 0.01 M Tris, 0.005 M EDTA, 0.005 M $MgCl_2$ at pH 7.0. The homogenate was centrifuged for 2 minutes at 600 × *g* to remove intact cells and cellular debris. The supernatant fluid was recentrifuged for 45 minutes at 20,000 × *g* in an International centrifuge. The clear supernatant fluid containing hexokinase activity (Table I) was used for the assays. Glucose determinations by the method of Nelson and Somogyi (20) showed only negligible amounts of free sugar present (less than 5 mg per 100 ml). Protein determinations showed the presence of 2.97 g of protein with a total hexokinase activity of 7800 units, assayed with glucose as a substrate.

2. Kidney Hexokinase—Fresh rat kidneys from two or three rats (approximately 6 g of tissue) were homogenized in a VirTis

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[1] The abbreviation used is: EDTA, ethylenediaminetetraacetic acid.

TABLE I

Distribution of hexokinase activity in tissue homogenates

Tissue	Centrifugation*		Units of hexokinase recovered			Amount in supernatant
	Speed	Time	Homogenate	Sediment	Supernatant	
	× *g*	*min*				%
Rat kidney	20,000	45	1,600	60	1,090	64
Rat liver	20,000	45	10,000	2,500	7,800	78
Rat intestine	800	30	13,000	1,800	11,000	85
	20,000	30	10,000	8,500	1,000	10

* After an initial centrifugation at 600 × *g* for 2 minutes to remove unbroken cells and other debris.

"45" homogenizer for 5 minutes with the buffer described above. A crude kidney hexokinase was obtained in the supernatant fluid after centrifuging the homogenate at 20,000 × *g* for 45 minutes (Table I). This preparation was stable for 2 to 3 weeks at −15°. A total activity of 1090 units in 0.65 g of protein was recovered.

3. Intestinal Hexokinase—Immediately after a rat was killed, the entire intestinal tract was removed and cleaned by flushing with ice-cold water. After all the contents were removed, the intestine was slit longitudinally and washed in cold phosphate buffer at pH 6.8. The tissue was cut into three or four pieces, and each was homogenized by hand with 2 volumes of cold phosphate buffer at pH 6.8. A loosely fitting glass homogenizer (21) was used so that only the mucosa was ruptured, the muscular layer being left intact. The homogenate was centrifuged at 800 × *g* for 30 minutes to remove the heavy material of the muscular layer. The supernatant fluid was used in the hexokinase assays (Table I). Intestinal mucosa has been shown to have mainly a particulate hexokinase (22). The supernatant fluid contained 4 g of protein with a total activity of 11,000 units. This preparation was found to be stable for 2 to 3 weeks if stored at −15°.

RESULTS AND DISCUSSION

To determine the extent of interference with the hexokinase assay by ATPase and other phosphatases, control experiments were carried out, the results of which are shown in Table II. From these data it can be seen that the activity of contaminating enzymes was low compared to hexokinase activity, and was further inhibited by the presence of fluoride at a concentration equal to that of the magnesium chloride. Some inhibition of hexokinase by fluoride is also indicated. The solutions containing the enzymes were frozen after their preparation and thawed before use. This procedure considerably decreased the activity of phosphatases without markedly reducing hexokinase activity (17). In subsequent assays it was determined that, in the absence of substrate, acid production caused by interfering processes was almost entirely absent and was therefore neglected. In those instances in which the test substance proved to be either inert or a very poor substrate, increasingly large amounts of the enzyme preparation were used in order to induce the reaction to proceed. Consequently, acid production resulting from ATPase activity was greater in these cases, but was never as much as 10% of the total acid produced in the presence of even the poor substrates. This was considered to be within the limits of experimental error under these circumstances, and the blank values were neglected. To this extent, however, the Michaelis constant (K_m) values reported for poor substrates such as gulose and talose are not entirely accurate.

The results of the substrate specificity studies are shown in Tables III and IV. Glucopyranose was used as the reference substrate, inasmuch as glucose is the physiological substrate for the tissues studied. Liver, however, may be taken as a partial exception to this, since fructose has been shown to be well utilized by this tissue (8) and, as previously noted, the presence of a unique fructokinase has been well established. Studies of aqueous solutions of some free aldohexoses have shown the pyranose form to be the predominant form present (23), and the assumption has been made that this holds true for all the aldohexoses. The points at which the sugars studied differ in structure from glucose have been indicated in Table III.

Values recorded for the Michaelis constants (K_m) were calculated from graphs by the method of Lineweaver and Burk (24). Comparison of K_m values obtained with enzymes isolated from different sources may provide information regarding the identity of the enzymes. The relative maximal rates of the reactions can be used to compare the behavior of a given enzyme toward a variety of substrates. This value was obtained from the expression

$$\text{Relative maximal rate} = \frac{V_{max}\ (\text{substrate})}{V_{max}\ (\text{glucose})}$$

The phosphorylation coefficient (25) is also useful in evaluating hexokinase activity. This coefficient was calculated from the expression

$$\text{Phosphorylation coefficient} = \frac{V_{max}\ (\text{substrate})}{V_{max}\ (\text{glucose})} \times \frac{K_m\ (\text{glucose})}{K_m\ (\text{substrate})}$$

It serves as an indication of the sensitivity required in test conditions and also gives some indication of the suitability of a substance as a substrate for a hexokinase.

TABLE II

Effect of endogenous metabolites, phosphatases, and fluoride on hexokinase assay of enzyme preparations from normal rat tissues

Tissue preparation	Substrate	Acid equivalents produced per minute (× 10^8)				
		Complete system*	−Substrate	−Fluoride	−Substrate −Fluoride	−Fluoride −ATP
Rat liver†	Glucose	38	8	54	12	0
	Glucose 6-phosphate	7	7	34		0‡
Rat kidney†	Glucose	51	9	72	18	5
	Glucose 6-phosphate	4	7	23		7
Rat intestine†	Glucose	74	16	84	23	0
	Glucose 6-phosphate	14	7	8		0‡

* Complete systems contained enzyme, 0.02 M $MgCl_2$, 0.002 M EDTA, 0.02 M potassium fluoride, 0.002 M ATP, and 0.0004 M substrate. Incubations were carried out at 30° and pH 7.4 for 4 minutes.

† Fresh supernatants prepared as in Table I.

‡ Increase in pH of 0.05 to 0.1 unit in 15 minutes.